

# Morphology and ecology of seedlings, fruits and seeds of Panama: Bixaceae and Cochlospermaceae

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## CONTENTS

Introduction .....	161
Methods .....	161
Bixaceae .....	162
Cochlospermaceae .....	166
Discussion .....	169
References .....	171

**SYNOPSIS.** Seedlings, saplings, fruits and seeds of *Bixa urucurana* (Bixaceae) and *Cochlospermum vitifolium* (Cochlospermaceae) are described, and ecological data on these stages summarized, as part of the ongoing *Seedling Flora Project*, centred on Barro Colorado Island, Panama. Data from these taxa and new seedling characters are used to discuss the relationship between the two families. The presence of extra-floral nectaries at leaf nodes along the stem and 'pearl bodies' on leaves, two ecologically important characters not described in standard floras, are discussed.

## INTRODUCTION

The aim of the *Seedling Flora Project*, initiated in 1985, is to produce an illustrated flora of seedlings, saplings, fruits and seeds for the neotropical forest centred on Barro Colorado Island, Panama (see Garwood & Humphries, 1993). In this account, two species are described, *Bixa urucurana* Willd. (Bixaceae) and *Cochlospermum vitifolium* (Willd.) Spreng. (Cochlospermaceae), which are rare on Barro Colorado Island (BCI) but common in other parts of central Panama. Although the two families are treated separately in the *Flora of Barro Colorado Island* (Croat, 1978), *Flora of Panama* (Robyns, 1967a, b; D'Arcy, 1987), and the *Flora neotropica* (Poppendieck, 1981), they are closely allied and often combined into one family, the Bixaceae (Corner, 1976; Cronquist, 1981).

## METHODS

Seeds were collected in central Panama, and sown while fresh under sun and shade conditions in a screened growing house on Barro Colorado Island. Seedlings were photographed, observed for fresh characters, and harvested at irregular intervals; several individuals were grown to sapling size. Each seed collection has a unique collection number: voucher specimens and the seedlings grown from that collection are lettered sequentially according to date of collection or har-

vest, e.g. 1784A (adult voucher), 1784B-G (seedlings). Adult voucher specimens are deposited among the following herbaria: F, BM and PMA. All seedling, fruit and seed specimens described are currently at BM, where seedling voucher specimens and fruit and seed samples will be deposited; duplicates of seedlings will be distributed to other herbaria.

Descriptions are based on photographs and notes of fresh specimens and on dry and preserved material from the collections described above, supplemented with general information from published floras. Taxonomic references used throughout the descriptive parts are summarized after the notes on family habit and distribution; references are cited in the fruit and seed descriptions only when they are the sole source of specific information; those used in the ecology section are cited in the text.

For each species, information is stored in a detailed database and output in a standard format that will be used for all 700 species in the *Seedling Flora Project*. Descriptive terms are being standardized across all families, but generally follow common usage. See de Vogel (1980) for definitions of seedling-specific terms. The following less conventional terms are used: length of pubescence or size of other surface features, minute (< 0.1 mm), short (0.1–0.5 mm), long (0.5–1.0 mm), very long (> 1.0 mm). Leaf nodes are numbered sequentially from the first leaf-bearing node above the cotyledons. A more detailed account of seed germination for all species is being prepared (Garwood, in prep.). In this account, the median time until germination is given, rather than the mean, because the distribution of germination time is highly skewed.

## BIXACEAE

**HABIT AND DISTRIBUTION.** Shrubs or trees. Neotropical, but the cultivated *Bixa orellana* L. is planted throughout the tropics; one genus and five species, two species in Panama and one or two species known from BCI (see below).

**TAXONOMIC REFERENCES.** Macbride (1941), Standley & Williams (1961), Robyns (1967a), Dathan & Singh (1972), Baer (1976), Corner (1976), Croat (1978), Molau (1983).

### *Bixa* L.

**TAXONOMIC NOTES.** Five species of *Bixa* are present and distinct in the Amazon basin (Macbride, 1941; Baer, 1976; Molau, 1983), including the widely cultivated *B. orellana* L. sensu stricto and its cultivars. Typical examples of *B. urucurana* Willd. and *B. orellana* L. occur throughout Central America, but intermediate forms have been reported (Baer, 1976) and Central American floras have combined the two taxa or ranked them as varieties of *B. orellana* L. sensu lato (Standley & Williams, 1961; Robyns, 1967a). See Dempsey & Garwood (1994) for further discussion of these two taxa.

The BCI taxon, described as *B. orellana* L. by Croat (1978), is probably *B. urucurana* Willd. Its distribution along the shoreline of BCI (Croat, 1978), where lake levels fluctuate greatly throughout the year, is consistent with the habitat of *B. urucurana* but not *B. orellana*. *B. urucurana* is usually found along stream and river banks and in seasonally inundated or periodically brackish low areas, whereas *B. orellana* does not tolerate waterlogged soils (Baer, 1976). In addition, the only *Bixa* seedlings I have encountered on BCI (Garwood 2439) were growing on a sandy beach at the mouth of a small stream. One BCI specimen (Croat 12294) has been identified as *B. urucurana* (Baer, 1976), but I have not verified others listed in Robyns (1967a) and Croat (1978). However, it would be surprising if the commonly cultivated *B. orellana* has never been planted on BCI, as many ornamental and food plants have been cultivated in the laboratory clearing and older settlement sites.

### *Bixa urucurana* Willd., *Enum. pl.*: 565 (1809).

Fig. 1.

**HABIT AND DISTRIBUTION.** Small tree, to 10 m tall, of moist to wet lowland forest, usually along streams, rivers or other inundated areas. Brazil and Peru to Nicaragua or Guatemala.

**COLLECTIONS.** **Panama.** Colón: Gamboa, along shoreline of Rio Chagres, Garwood 1830A (BM, F, PMA, adult vouchers), Garwood & Rand 2085A (no voucher, same tree as Garwood 1830A); Barro Colorado Island: shoreline, Garwood 2439 (seedlings); 7 seedlings to 69 cm tall examined (Garwood 1830B–D, 2085B–C, & 2439).

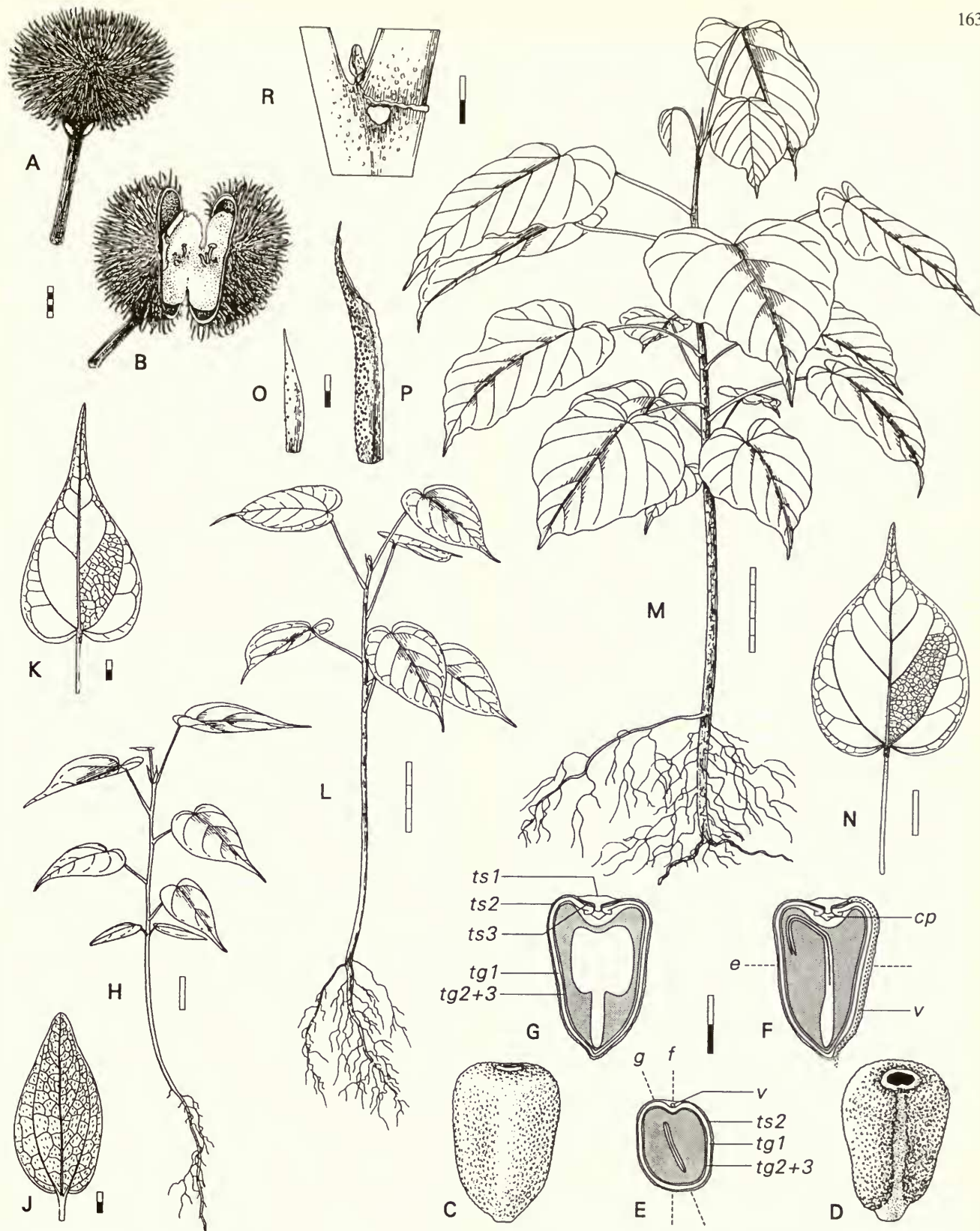
#### Fruits

**Infructescences** terminal; loosely branched panicle-like thyrse to about 22 cm long, with 1–3 fruits usually maturing per branch. Rachis to about 22 cm long; branches to about 5 cm long; pedicels 1.5–2.0 cm long with 5 large glands about 2.5 mm tall below calyx scars; all stems densely scaly. **Receptacles** undeveloped. **Stipes** to 1 mm long, straight, circular in t.s., scaly, remaining attached to capsule. **Fruits** capsules, dry

(with slightly fleshy seeds); from superior ovaries, with corolla and sepal scars inconspicuous among 5 large, extrafloral glands at base; carpels 2; locules 1. Capsules papery to woody, indehiscent or tardily loculicidally dehiscent; partially septate; 15–30(45) × 15–30 × 10–25 mm, (including spines); straight; circular to transversely elliptic in outline, circular in t.s.; margins entire; base widely rounded to truncate; apex widely rounded to truncate, with a terminal cluster of tightly packed short spines; densely covered with large, stiff spines, to 5 mm tall, with enlarged bases usually touching; surface medium to dark brown to red-brown, dull, with short weak spines < 0.5 mm tall among bases of larger spines; sparsely to moderately scaly, especially around bases of larger spines; scales peltate, orange-brown to brown, ± sessile to stalked. Seeds 6–12, central, touching along 1–2 sides, slightly deformed by neighbours; long axis of seed oblique to central axis of fruit. **Placentae** parietal; each a 2 mm wide dark band on lower half of endocarp, with seeds in 2 rows, and dark band narrowing above seeds and continuing to apex. **Funicle** about 2 mm long, curved to coiled, cylindrical, persistent on placentae, flared apically into shiny, 2-lobed appendage below seed, 1.5–2 mm long, each lobe a series of undulating compressed folds. **Septa** marginal, extending full-length of fruit but < ¼ distance to centre, about 2 mm tall throughout its length, solid basally but perforated apically, located under placenta but hidden by endocarp. **Valves** 2, dehiscent from apex if tardily dehiscent, spreading apart slightly, remaining attached at base. **Fruit wall** thin, about 0.5 mm wide (excluding larger spines), 3-layered, endocarp separating from outer fruit wall at maturity. **Exocarp** very thin, about 0.05 mm wide, ± crustaceous, dark brown. **Mesocarp** thin, about 0.25 mm wide, forming most of septa, ± cartilaginous from numerous reticulate, tough fibres, which continue into bases of larger spines; spaces between fibres filled by ± papery matrix, which is compressed, shiny and mottled with orange-brown on inner surface, medium brown with cream-coloured fibres. **Endocarp** very thin, ≤ 0.05 mm wide, dry-membranous, dark brown to orange-brown; inner surface rough, glabrous, dull, dark brown to orange-brown.

#### Seeds

Seeds 3.7–5.1 × 3.5–4.3 × 3.0–3.8 mm; sarcotestal; anatropous; widely obovate or widely obtriangular in outline, compressed except subcompressed apically, mostly ± elliptic in t.s., with both faces often concave; margins entire; base moderately acute; apex truncate; apical cap over chalazal foramen moderately raised, circular, ≈ 2 mm wide, with light brown outer ring and black centre, both easily dislodged; deep medial groove extending > ¾ length of seed, from hilum to apex along raphe; outer surface densely pustulate when dry, papillate when moistened, rough between pustules at higher magnification, glabrous, slightly glossy when dry, medium orange-brown or red-brown when dry, papillae yellow when moistened; if sarcotesta eaten or removed, then outer surface smooth, smooth at higher magnification, glabrous, glossy, medium brown to orange-brown, except dark black-brown at base around micropylar regions. **Aril** absent. The funicular appendage (see above), which Corner (1976) describes as a vestigial aril, remains firmly attached to the funicle. **Sarcotesta** hard when dry, fleshy when moistened; with large oil cells resin-like when dry, becoming soft and waxy when moistened, but drying firm and waxy; completely surrounding seed; initially medium brown to orange-brown



**Fig. 1** *Bixa urucurana* Willd. Fruit: A, indehiscent capsule; B, forcefully opened capsule. Seed: C–D, two views; E, t.s. (through plane 'e' in F); F, medial l.s. (through plane 'f' in E); G, oblique l.s. (through plane 'g' in E). Seedling: H, older seedling; J, cotyledon; K, first leaf. Saplings: L, young sapling; M, older sapling; N, leaf at about node 17; O, stipule at about node 24; P, stipule at node 45; R, gland at about node 40. Scale bars: black and white, 1 mm units; white only, 1 cm units. Symbols: outer to inner layers of testa (ts1–ts3) and tegmen (tg1–tg3); vascular trace (v); chalazal plug (cp); endosperm (shaded); and cross-sectional planes for E, F, and G (dashed lines: e, f and g, respectively).

when dry, becoming yellow or orange-yellow when moistened (and remaining so upon redrying); initially  $\pm$  pusticulate when dry, becoming  $\pm$  papillate when moistened (and remaining so); developing from entire testa. *Hilum* subbasal in medial groove, exposed, slightly recessed to flush, sometimes raised around end of vascular bundle, medium orange-brown, slightly lighter than surrounding sarcotesta, black-brown if tegmen exposed, usually indistinct and ill-defined, sometimes distinct, elliptic and  $\approx$  1 mm long when much of sarcotesta adheres to funicle, often with irregular patch of tegmen exposed over the micropylar region. *Micropyle* basal, not visible. *Chalazal foramen* apical, not visible until apical cap removed, conspicuous on tegmen, round,  $\approx$  1.25 mm wide; closed by black chalazal plug, flat-topped,  $\pm$  shallowly conical,  $\approx$  0.5 mm wide, on a brown,  $\approx$  1.5 mm wide disk, an extremely complex structure formed from specialized chalazal tissue (hypostase) and tegmen. *Endosperm* thick, encasing embryo, hard, rapidly becoming soft once moistened, starchy (Corner, 1976), cream-coloured to white. *Embryo* large, to 5 mm long, central, with cotyledons in plane oblique to medial plane through raphe, straight except abruptly curved at apex of cotyledon under chalazal plug, spatulate, flattened, yellow or yellow-green; axis well-developed, completely exposed; cotyledons well-developed, flat, often slightly curved, thin, ovate in outline, cordate at base; plumule rudimentary. *Vascular bundle* lateral, unbranched, very thin, sometimes exposed at hilar end, passing through sarcotesta in the medial groove of the raphe, sometimes visible through sarcotesta, terminating apically in chalazal cap. *Seed coat* thick, mostly 0.125–0.25 mm wide, except to 1.0 mm wide over chalaza, bony, with fleshy sarcotesta, exotegmic. *Testa* thin when dry, thicker in medial groove,  $\pm$  thick when moistened, resin-like when dry, a fleshy sarcotesta when moistened, mostly 1-layered except 3-layered at apex around chalazal foramen; outer layer very thin, crustaceous, only evident as apical cap over chalazal foramen, light brown with black centre; middle layer (see sarcotesta above) less developed beneath apical cap; inner layer thick, bony, dark-brown, only evident below apical cap, tightly appressed to tegmen and lining the chalazal foramen. *Tegmen* thick, bony, quickly becoming leathery during imbibition, impermeable on outer surface but highly permeable on inner surface, 3-layered; outer layer thick,  $\pm$  bony, cream-coloured to light grey, inflexed apically forming chalazal foramen, with a very thin dark brown inner band that becomes thick at base around micropylar area and forms a thick dark internal ring around chalazal foramen; middle layer very thin,  $\pm$  papery, light brown, except thick and spongy around chalazal plug, splitting during imbibition and partially adhering to outer and inner layers; inner layer very thin,  $\pm$  papery, medium brown, except  $\pm$  thick, bony and black-brown beneath chalazal plug, separating from middle layer during imbibition, becoming leathery (except under chalaza), and adhering to endosperm.

#### *Seedlings and saplings*

Seedlings phanero-epigeal with cotyledons haustorial during germination, then photosynthetic.

**DEVELOPMENT.** Hypocotyl elongates into loop, the cotyledons emerge from seed, sometimes not fully escaping seed. Hypocotyl straightens.

**ROOTS.** *Primary root* circular in t.s., curved to sinuous, light

brown; surface texture and colour between hypocotyl and root change slightly and gradually around collet. *Secondary roots* sinuous, scattered along primary root. *Root hairs* not evident. *Sapling root system:* taproot long-tapering, very thick for much of length; secondary roots mostly very thin and common, a few moderate-sized; rootlets very fine to fine and numerous.

**STEMS.** *Hypocotyl* 34–38  $\times$  1–2 mm, circular in t.s.; smooth, drying longitudinally wrinkled; glabrous; green. *Epicotyl* 1–5  $\times$  0.5–2 mm, circular in t.s., smooth, sparsely minutely scaly, green. Scales peltate,  $\pm$  sessile, erect, light orange-brown. *Cataphylls* absent. *Internodes* 1–10, 3–17 mm long; later internodes to 40 mm; circular in t.s.; smooth; glands absent on internodes 1–10, present below the stipule scar and well-developed on most internodes  $\geq$  20, secreting nectar 3–4 internodes below youngest leaf, to 1 mm tall, widely obovate, with apex rounded to obcordate, light brown-green when fresh, drying light brown on glabrous raised pad twice width of gland and darker brown than surrounding stem; sparsely scaly at internodes 1–5, moderately scaly through internode 20, densely scaly at later internodes; slightly pusticulate at early internodes, often moderately to densely pusticulate at later internodes, pustules often still filled with dark orange-brown fluid on dry specimens. Scales peltate,  $\pm$  sessile, light orange-brown,  $\approx$  0.05 mm in diameter at first internode to 0.10 mm in diameter at later internodes,  $\pm$  circular with entire to irregular margins. *Older stems* dark brown-green to dark grey-brown, solid basally, often hollow apically, shallowly furrowed, rough and often glabrous with age as initial bark surface fragments; wood cream-coloured. *Lenticels* first appearing on older stems  $\approx$  2–5 mm wide, common on older stems 6–8 mm wide; mostly  $\approx$  0.5 mm long, raised, initially elliptic to round, widening with age, cream-coloured on darker stems. *Buds:* Cotyledonary buds hidden or slightly protruding to 0.2 mm out of axils, slightly protruding above cotyledon scars, glabrous. Lateral buds protruding  $\approx$  0.2 mm out of axils at early nodes, to 1 mm at later nodes; glabrous at early nodes to moderately or densely scaly at later nodes; enclosed within at least 2 widely to very widely triangular scale leaves. Terminal buds covered by stipules, glabrous at nodes 1–10, gradually becoming densely scaly at later nodes.

**COTYLEDONS.** Two, opposite, foliaceous, simple, petiolate, estipulate, emergent from seed, spreading apart, persistent until at least node 5 matures. Blades 15–18  $\times$  8–10 mm; straight, flat, ovate; apex acute to narrowly rounded; base  $\pm$  cordate; margins entire. Blades densely thick-lined below, each to 0.5 mm long, parallel to long axis of cotyledon, light brown-orange, faintly pellucid and yellow-brown against strong light; faintly pellucid thick-lined above against strong light, otherwise scarcely visible; glabrous above and below; green. *Venation* palmate, 3-veined; brochido-actinodromous, basal and perfect. Primary veins 3; fine to moderate-sized; moderately raised above when dry, prominently raised below; central primary vein moderate-sized, straight to sinuously apically; lateral primary veins basal, fine,  $>$   $\frac{3}{4}$  length of blade, curved or slightly arched, diverging at narrowly acute angles, looped, obtusely to perpendicularly joined to secondaries of midvein. Secondary veins fine; 10–18 per cotyledon, 4–5 along midvein and 3–4 along each lateral primary vein; alternate along midvein, marginal along lateral primary veins;  $\leq$   $\frac{1}{2}$  length of blade, longest centrally along midvein; arched; diverging at mostly narrowly acute angles; looped,

variously joined to superadjacent secondaries; slightly raised above, slightly raised to flush below. Inter-secondary veins occasional. Tertiary veins reticulate within intercostal area, looped within marginal area. *Petioles* 2–3 mm long, half-circular in t.s., channelled, often warty along margins and at apex above.

**LEAVES.** Alternate and spiral; simple; long-petiolate, stipulate. Leaf blades 22–25 × 12–13 mm at first node; 25–40 × 14–20 mm at nodes 2–5; to 229 × 168 mm at later nodes; straight; ovate at nodes 1–5, becoming widely ovate at later nodes; apex long-acuminate at nodes 1–5, becoming acuminate or short-acuminate at later nodes; base cordate at nodes 1–20, usually becoming emarginate, truncate or widely rounded at later nodes; margins entire. Blades dark green above, lighter below; raised between the veins when fresh; papery; usually densely minutely light orange-brown or green-brown punctate on blade below at early nodes, becoming dark brown punctate at later nodes, sometimes with thick dark brown-orange lines on veins below at later nodes, each punctation usually 0.05–0.10 mm long, irregular, circular or ± elliptic in outline, usually yellow-green pellucid against strong light at early nodes to light orange-brown pellucid at later nodes, sometimes opaque and dark brown-orange at later nodes, often associated with short thin or thick pellucid canals, sometimes branched; sometimes moderately punctate above, but usually pellucid dots scarcely visible above except against strong light; glabrous to sparsely minutely scaly below on veins and blades at nodes 1–5, becoming moderately scaly at later nodes; glabrous to sparsely minutely scaly above on veins and blades at nodes 1–5, becoming mostly sparsely scaly at later nodes; glabrous along margin. Scales peltate, ± sessile, light orange-brown, mostly ≤ 0.05 mm in diameter on blade, to 0.10 mm on veins below, ± circular with entire to irregular margins. *Young leaves* spreading open almost immediately, glabrous or sparsely scaly below at early nodes to densely scaly below at later nodes; initially densely pustulate above, with shiny coating above apparently secreted by pustules when leaf about  $\frac{1}{4}$ – $\frac{3}{4}$  expanded, surface becoming ± dull again when full-size, dark green-brown, becoming dark brown-green, rigid, descending, produced continually, often before previous 1–3 leaves full-size. *Venation* palmate, 5-veined; brochido-actinodromous, basal, perfect. Primary veins 5; moderate-sized; moderately raised above, prominently raised below; central primary vein straight; lateral primary veins basal, thinner than midvein, inner pair of lateral primaries  $\frac{1}{2}$ – $\frac{3}{4}$  length of blade, arched, diverging at moderately acute angles, looped, acutely to perpendicularly joined to secondary vein from midvein; outer pair <  $\frac{1}{2}$  length of blade, arched, diverging at ± perpendicular angles, looped to diffusely looped, perpendicularly to obtusely joined to secondary vein from inner lateral primary vein. Secondary veins moderate-sized along midvein, fine along lateral veins; 4–6 along midvein and 2–3 along each inner lateral vein on leaves at first node, 4–8 along midvein and 2–4 along each inner lateral vein at nodes 2–5, 8–15 along midvein and 2–8 along each inner lateral vein at nodes ≥ 12; alternate to subopposite along midvein, on outer (exmedial) side of lateral veins; ≤  $\frac{1}{3}$  length of blade, longest centrally along midvein; mostly arched, often hooked apically along midvein and distally along lateral primary veins; diverging at moderately acute angles; looped, sometimes diffusely looped centrally along lateral primary veins, mostly perpendicularly joined to superadjacent secondary vein; slightly raised above,

moderately raised below. Inter-secondary veins absent to occasional in intercostal areas along midvein. Tertiary veins looped within marginal area, ± reticulate within intercostal area at nodes 1–5, becoming straight-percurrent and oblique to midvein near margin and convex-percurrent near midvein at later nodes. *Petioles* 10–140 mm long, 10–20 mm long at nodes 1–5; straight, circular in t.s.; often drying channelled above, enlarged at base, pulvinate at apex, medium yellow-green to green with medium brown pulvinus; sparsely to moderately pustulate, sparsely minutely scaly at early nodes becoming moderately scaly at later nodes, pulvini usually densely pustulate and densely scaly at later nodes. *Stipules* paired; 2–5 mm long at nodes 1–5, to 19 mm long at later nodes; simple, narrowly triangular, with long acuminate apex; quickly deciduous, papery; glabrous at early nodes to densely scaly at later nodes; green becoming light-brown; leaving pair of conspicuous scars above petiole, perpendicular to stem, each >  $\frac{3}{4}$  width of stem.

**SAP.** Not evident in freshly cut leaves, bark, or roots, but slowly oozing out around central pith of cut stem, drying cream-coloured to medium orange-brown and resin-like.

**ODOUR.** Not distinctive.

**ARCHITECTURE.** Trunk axis monopodial. Initial axis orthotropic. No branches formed on plants ≤ 70 cm tall, but elongated lateral buds (to 4 mm long) on largest individual suggest that sylleptic branches might soon be produced. Leaves held ± horizontal to descending.

#### Ecology

**PHENOLOGY.** Central American *B. urucurana* flowers in the late rainy season September–December, with fruit developing during the following dry season. Fruits from my Panamanian collections were dark brown and dry in April and May.

**DISPERSAL.** When ripe, the dry capsule is dark brown with stiff spines, and probably indehiscent (Baer, 1976) or at most tardily dehiscent. Seeds within the dry, indehiscent fruit are also dry and dark orange-brown to red-brown, but the sarcotesta becomes soft, papillate and bright yellow when moistened. Dispersal mode is unknown. Seeds of the genus *Bixa* are usually assumed to be bird-dispersed because of the bright red or red-orange sarcotesta visible in the dehiscent capsule, but Baer (1976) notes there are no observations of birds taking the seeds. In the indehiscent fruits of *B. urucurana*, the duller orange-brown to red-brown seeds are not visible at maturity and are unlikely to attract birds. Given its riverside habitat, suggestions of fish-dispersal (van Roosmalen, 1985) or water-dispersal (Baer, 1976) are not unreasonable. In addition, the spiny, dry, brown indehiscent fruits hiding pulp-covered seeds are reminiscent of *Apeiba membranacea* Spruce ex Benth. (Tiliaceae), which is mammal-dispersed.

**GERMINATION.** Seeds of *B. urucurana* germinated slowly (22–38 weeks) at low percentages (5–12%) in both sun and shade in the growing house. Baer (1976) failed to germinate seeds of numerous samples of *B. urucurana*, although those from *B. orellana* sensu stricto germinated easily. Seeds collected from unopened fruit of the cultivated *B. orellana* sensu stricto have high moisture content (≈ 45%, fresh weight basis [FWB]) and permeable seed coats (Goldbach, 1979), and germinate rapidly (< 1–3 weeks; Garrard, 1955; Goldbach,

1979; Chin et al., 1984). When seeds are air-dried, they become impermeable, moisture content drops ( $\leq 10\%$  FWB), and germination becomes sporadic over  $> 1$  year. Under natural conditions, the chalazal plug must become loosened before imbibition and germination can occur, but this requirement can be circumvented if seeds are scarified by cutting off the micropylar tip of the seed coat below the radicle (Goldbach, 1979). The proportion of impermeable seeds in a collection varies from 0% (Garrard, 1955) to  $> 50\%$  (Goldbach, 1979), depending on seed moisture content, period of drying, and possibly cultivar used. My collections of *B. urucurana* had low seed moisture contents (6–10%, FWB), suggesting that the seed coats were impermeable at time of dispersal. Seeds of *B. orellana* air-dried to about 10% moisture content (FWB) and stored for 12 months in the laboratory at 23°C retained high viability (95% of initial viability); those dried to about 4% moisture content had slightly lower viability (82% of initial values) over the same period (Goldbach, 1979). Baer (1976) also reports high viability after 1 year, whereas Garrard (1955) found viability was completely lost after 5 months. The latter may reflect the absence of seeds with impermeable coats in that collection.

## COCHLOSPERMACEAE

**HABIT AND DISTRIBUTION.** Trees, shrubs, subshrubs or rhizomatous herbs. Tropical; two genera and 15 species, one genus and two species in Panama, and one species known from BCI.

**TAXONOMIC REFERENCES.** Robyns, (1967b), Dathan & Singh (1972), Corner (1976), Croat (1978), Poppendieck (1980, 1981).

### *Cochlospermum* Kunth

**HABIT AND DISTRIBUTION.** Small trees, shrubs, or subshrubs. Pantropical, mostly South American; 12 species, two species in Panama, one species known from BCI.

***Cochlospermum vitifolium* (Willd.) Spreng., Syst. 4(2): 406 (1827).**

Fig. 2.

**HABIT AND DISTRIBUTION.** Small sparsely branched trees, 3–12 m tall, of dry to moist lowland forests or savannas, common in young secondary forest, and along frequently burned roadsides. Mexico to Bolivia, northern Brazil and West Indies; introduced into Palearctica.

**COLLECTIONS.** **Panama.** Colón: Gamboa, beginning of Pipeline Road, *Garwood & Lighton* 1784A (F, PMA, adult vouchers); same locality, *Garwood* 2941A (BM, fruit voucher); Barro Colorado Island: *Garwood* 3060A (BM, seed voucher); 20 seedlings to 81 cm tall examined (*Garwood* 1784B–G, 2941B, 3060B).

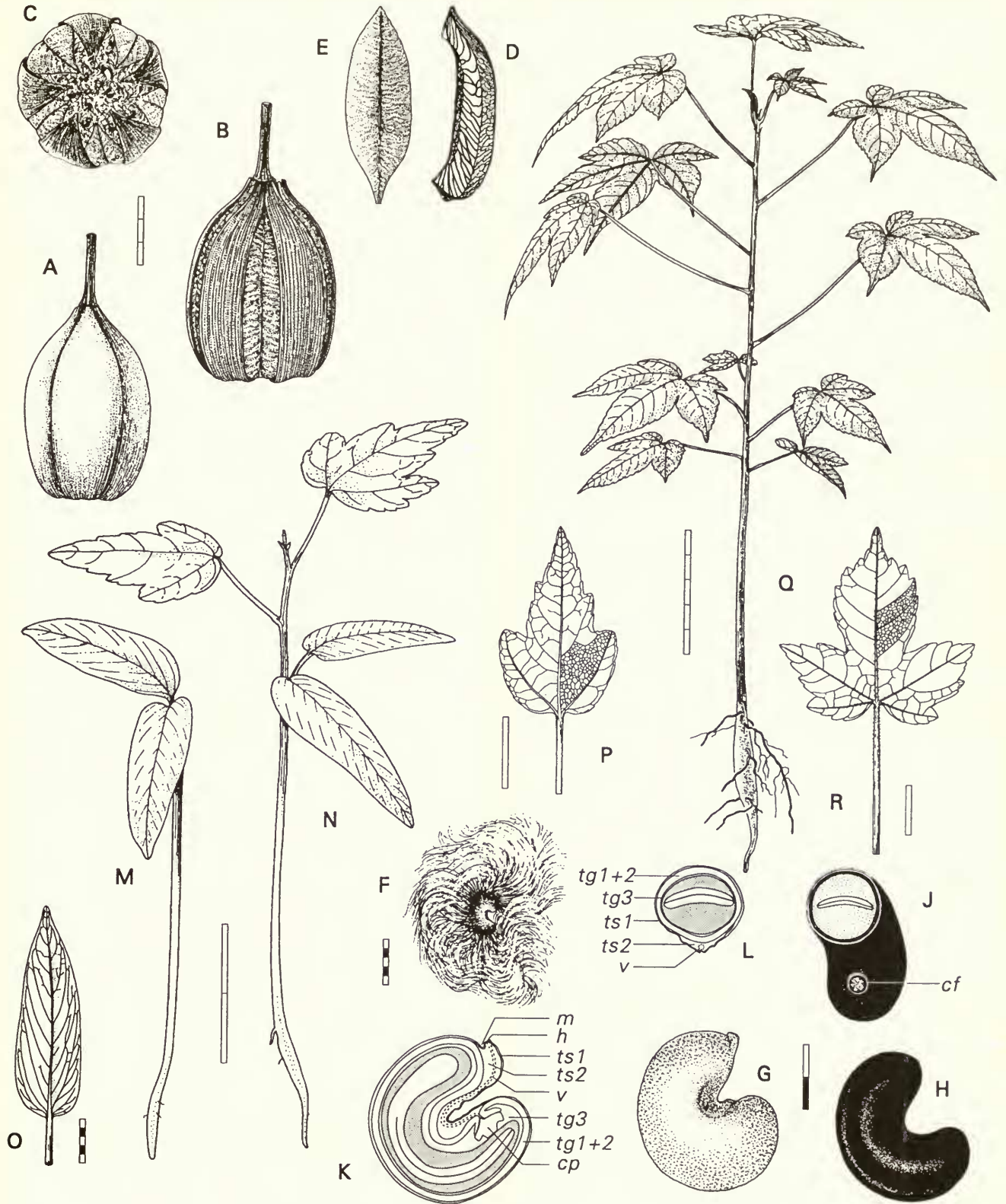
#### Fruits

**Infructescences** terminal; sparsely branched panicle-like thyrses, with 1(–2) fruit maturing per branch, capsules suberect to pendent. Stems woody, glabrous or pubescent; peduncles 2–5 cm long, rachis and branches about 3–20 cm

long, pedicels 3–4 cm long. **Receptacles** undeveloped. **Stipes** absent. **Fruits** capsules, dry; from superior ovaries, with withered persistent sepals, to 28 mm long at base; carpels 5; locules 1. Capsules papery to woody, locucially and septically dehiscent (outer and inner valves, respectively); partially 5-septate; (40–)70–90(–110)  $\times$  35–70  $\times$  35–70 mm; straight; obovate or widely ovate or elliptic in outline, circular in t.s.; margins entire; base truncate to short-attenuate; apex truncate and centrally depressed; surface dark brown or grey, dull, densely longitudinally narrowly multi-ridged, moderately to densely minute- to short-pubescent; hairs simple, erect. Seeds numerous, intermediary, touching along compacted cotton-like hairs but seed bodies separate, compressed  $\pm$  laterally; long axis of seed parallel or oblique to long axis of fruit; at maturity, free within locule. **Placentae** intruded parietal; each cylindrical, running  $\pm$  full length of fruit,  $\approx 50$ –60  $\times$  5–6 mm, with numerous large funicular mounds, minute ovule scars, and aborted ovules and seeds. **Funicle** to 0.5 mm tall, straight, widely to very widely conical, persistent on placentae. **Septa** marginal, extending  $\frac{1}{2}$ – $\frac{3}{4}$  distance to centre. **Valves** 10, 5 outer and 5 inner, dehiscent from apex, spreading apart, each outer valve overlapping margins of adjacent inner valves except open at apex, outer valves remaining attached at base or by thread-like extension of placentae or sometimes falling; inner valves eventually falling out. **Fruit wall** thin, about 1.0 mm wide, 3-layered, endocarp separating from outer fruit wall at maturity. **Exocarp** thin,  $\pm$  woody, with tough closely spaced longitudinal fibres, dark brown or grey. **Mesocarp** thin on inner surface of outer valves, forming thin septa and thickened placentae, spongy to cobwebby, with conspicuous vascular fibres transverse to oblique and sinuous on valves and oblique and often branched on septa, cream to light brown. **Endocarp** very thin, forming 5 separate elliptic inner valves, dry-membranous, translucent, dull, light brown or orange-brown; inner surface with central longitudinal ridge and numerous  $\pm$  reticulate ridges, glabrous, glossy. When fruit unripe, exocarp green.

#### Seeds

Seeds 4–5  $\times$  3–4  $\times$  1–2 mm; campylo-anatropous (Corner, 1976); C-shaped in outline, sometimes slightly coiled, circular in t.s.; margins entire; base eccentrically short-attenuate; apex rounded; outer surface rough except wrinkled in sinus, densely very long-pubescent except glabrous in sinus, with hairs to 14 mm long, erect, sinuous, white, fluffy and cotton-like, easily detached after dispersal; dull, mostly medium brown except red-brown or orange-brown or dark brown in sinus; exfoliating to reveal tegmen, then base rounded, outer surface smooth, minutely cellular at higher magnification, glabrous, glossy, black. **Aril** absent. **Sarcotesta** absent. **Hilum** basal and eccentric to subbasal, toward sinus, exposed, prominently raised on testa, not visible on tegmen after testa exfoliates, cream-coloured, lighter than testa, circular. **Micropyle** basal, centric, exposed but partially hidden by hilar mound, prominently raised on testa, only slightly raised on tegmen,  $\pm$  conical to cylindrical on testa, punctiform on tegmen. **Chalazal foramen** subapical in sinus, not visible on testa but conspicuous on tegmen, round, about 0.6 mm wide; filled by black chalazal plug, conical on 0.8 mm wide disk, similar in composition to tegmen. **Endosperm** thick, encasing embryo,  $\pm$  hard, oily (Cronquist, 1981), white. **Embryo** moderate-sized,  $\approx 4$ –6 mm long, central, C-curved,  $\pm$  spatulate when straightened, compressed; axis moderately



**Fig. 2** *Cochlospermum vitifolium* (Willd.) Spreng. Fruit: A, green, undehiscent capsule; B, dehiscent capsule, side view; C, dehiscent capsule, apical view; D, outer valve, with placenta; E, inner valve. Seed: F, complete seed with testal hairs; G, hairs removed to show surface of testa; H, testa removed to show surface of tegmen; J, partial seed, testa removed to show chalazal foramen in sinus; K, l.s. of seed without hairs; L, t.s. through sinus. Seedling: M, young seedling; N, older seedling; O, cotyledon; P, first leaf. Sapling: Q, sapling; R, leaf at node 4. Scale bars: black and white, 1 mm units; white only, 1 cm units. Symbols: outer to inner layers of testa (ts1–ts2) and tegmen (tg1–tg3); vascular trace (v); hilum (h); micropyle (m); chalazal plug and foramen (cp and cf); and endosperm (shaded).

developed, exposed; cotyledons moderately developed, flat, thin, entire; plumule rudimentary. *Vascular bundle* lateral in sinus, unbranched, thin, exfoliating with testa; passing through raphe, terminating subapically in chalazal foramen. *Seed coat* very thick, bony, exotegmic. *Testa* very thin,  $\pm$  thicker in sinus, crustaceous, loosely surrounding tegmen, often exfoliating, 2-layered except 3-layered in sinus; outer layer thin,  $\pm$  crustaceous, light brown except red-brown or orange-brown in sinus, densely long-pubescent (see above); middle layer absent except  $\pm$  thick in sinus, hard-spongy, cream-coloured; inner layer thin,  $\pm$  crustaceous, black. *Tegmen* very thick,  $\pm$  bony to glassy, 3-layered; outer layer very thin, waxy,  $\pm$  clear; middle layer thick, bony to glassy,  $\pm$  3-banded, with cream then brown then black bands; inner layer thin except thicker under chalazal foramen, cream-coloured, membranous to spongy, with abundant red-brown compressed globules (gum cavities).

#### *Seedlings and saplings*

Seedlings phanero-epigeal with cotyledons haustorial during germination, then photosynthetic.

**DEVELOPMENT.** Radicle emerges from hilar region and slightly elongates, as cotyledons absorb endosperm. Hypocotyl elongates into loop, then straightens, pulling cotyledons from seed. Cotyledons expand, sometimes not fully escaping seed, which is often carried upwards on tip of cotyledons. Cotyledons are usually fully expanded within 2 weeks of germination. Shoot rest period is short during the cotyledon stage, sometimes lasting  $< 1$  week in sun. Shade-grown seedling usually die without advancing past the cotyledonary stage. Growth is continuous in sun, with a new leaf initiated about every 1–2 weeks, often before the previous leaf has reached full-size.

**ROOTS.** *Primary root*  $\approx 30 \times 1$  mm, poorly developed in shade, circular in t.s., straight to sinuous, cream-coloured becoming brown; surface texture and colour between hypocotyl and root change slightly and gradually around collet. *Secondary roots* to 0.2–0.3 mm wide, sinuous, sparsely scattered along primary root. *Root hairs* appear quickly on primary root. *Sapling root system:* taproot with tuberous swelling (xylopodium), to  $50 \times 15$  mm, forming 10–20 mm below collet, developing in first year, produced on some seedlings only 12 cm tall; taproot long-tapering below swelling, thin to moderate-sized; secondary roots thin to moderate-sized, few to common; rootlets fine, few to common.

**STEMS.** *Hypocotyl*  $33\text{--}71 \times 0.5$  mm, circular in t.s.; slightly grooved apically below petioles; glabrous basally becoming densely minute-pubescent in apical  $\frac{1}{2}\text{--}\frac{1}{3}$ ; medium yellow-green, often medium red-brown in sun. Hairs simple, erect to ascending, curved, clear to cream-coloured. *Epicotyl*  $9\text{--}17 \times 0.5$  mm, circular in t.s., densely minute-pubescent, medium yellow-green to dark green. Hairs simple, erect to ascending, curved or sinuous or coiled, clear to cream-coloured. *Cataphylls* absent. *Internodes* 1–10, 2–17 mm long; later internodes to 65 mm; circular in t.s.; densely pubescent on side above petioles but glabrous to sparsely minute-pubescent on other side, glabrous to sparsely pubescent at later nodes, with abundant pearl bodies on youngest internode; medium yellow-green to dark green. Hairs simple, erect to ascending, curved or sinuous or coiled, clear to cream-coloured. Pearl bodies minute, globular, 0.05–0.075 mm in diameter, erect,

short-stalked, clear, usually drying orange-brown. *Older stems* medium grey-green then medium grey-brown, solid with small soft pith basally to hollow apically; wood cream to cream-brown, with  $\pm$  white rays, porous. *Lenticels* appearing on stems  $> 3$  mm wide, common on stems  $> 4$  mm;  $\leq \frac{1}{2}$  mm long, round, widening with age, slightly raised, dark brown, on lighter stems. *Buds:* Cotyledonary buds hidden in axils, usually inconspicuous above cotyledons scars, rarely protruding on older stems. Lateral buds hidden in axils at early nodes to protruding out of axils at later nodes, glabrous to slightly pubescent, enclosed within at least 2 scale leaves. Terminal buds naked, covered by stipules from several nodes, moderately pubescent.

**COTYLEDONS.** Two, opposite, foliaceous, simple, petiolate, estipulate, emergent from seed, spreading, persistent until nodes 2–7 mature (usually for 2–4 weeks, sometimes to 13 weeks). Blades  $24\text{--}26 \times 7\text{--}8$  mm; straight, flat, narrowly ovate; apex narrowly acute or acute; base obtuse or emarginate or truncate; margins entire. Blades glabrous above and below; green above, lighter below. *Venation* pinnate; eucamptodromous, sometimes brochidodromous in apical third. Midvein fine; straight to slightly sinuous; impressed above except slightly raised apically when dry, moderately raised below. Secondary veins moderate-sized; 16–18; mostly alternate except opposite at 2–4 basal veins;  $\frac{1}{3}\text{--}\frac{2}{3}$  length of blade, longest basally; slightly curved; diverging at narrowly acute angles; open, branching and terminating near or at margin; slightly raised to flush above, slightly raised to flush below. Inter-secondary veins occasional. Tertiary veins inconspicuous and reticulate. *Petioles* 4–5 mm long, straight, half-circular in t.s., moderately channelled, mostly glabrous below, densely minute-pubescent above, with abundant pearl bodies above.

**LEAVES.** Alternate and spiral; simple; long-petiolate, stipulate. Leaf blades  $21\text{--}33 \times 13\text{--}22$  mm at first node;  $18\text{--}67 \times 12\text{--}70$  mm at nodes 2–10; to  $190 \times 210$  mm at later nodes; ovate to widely ovate at nodes 1–2, becoming widely ovate to very widely ovate at nodes 3–10, mostly widely ovate to depressed ovate at later nodes; unlobed to palmately 3-lobed or 3-cleft at first node, becoming 3-parted, with central lobe largest and 2 large basal teeth becoming increasingly lobe-like at nodes 2–20, often 5-parted at later nodes, with central lobe at least slightly larger; apex of lobes mostly acute or acuminate at nodes 1–10, often long-acuminate at later nodes; base retuse or emarginate or cordate at nodes 2–15, mostly cordate at later nodes; margins  $\pm$  irregularly serrate at nodes 1–3, becoming  $\pm$  doubly serrate at later nodes. Teeth irregularly spaced and variably sized at nodes 1–10, becoming  $\pm$  regularly spaced at later nodes; mostly 4–15 per side at first node, to  $\approx 50$  per side at nodes 1–10, and to  $> 100$  per side at later nodes; margins mostly curved, proximal side longer than distal side; apex acute to short-acuminate; sinus angular. Blades green above, lighter below; flat between the veins when fresh; membranous; with pearl bodies common above and below on primary veins at nodes 1–10, especially basally above, and infrequent to common on primary and secondary veins at later nodes, but sometimes infrequent below; glabrous on blade above and below, glabrous to sparsely short-pubescent along margin; glabrous to sparsely short-pubescent on primary veins below at nodes 1–10, but only at base of primary veins above; glabrous to moderately short-pubescent on primary and secondary veins below at later nodes, but



glabrous or sparsely short-pubescent above along primary vein and densely pubescent at base; with short pellucid canals along margin drying harder than blade, canals absent or light yellow-orange at early nodes to mostly red-orange at later nodes; similar red-orange canals often conspicuous throughout blade of young leaves at later nodes. Hairs simple, erect to ascending, straight to curved, clear to cream-coloured. Pearl bodies minute, 0.05–0.075 mm in diameter, globular, short-stalked to sessile, erect, clear to white on immature leaves, becoming red-orange to brown with age. *Young leaves* plicate (lobes conduplicate-induplicate), densely pubescent, light green, with red-brown petioles, rigid, erect then  $\pm$  horizontal, produced continuously before or after previous leaf full-size. *Venation* palmate, 3- to 5-veined; actinodromous, basal, perfect and marginal. Primary veins 3 at nodes 1–3, 3 to 5 at later nodes; moderate-sized; impressed above, prominently raised below; central primary vein straight to slightly curved; lateral primary veins basal, diverging at moderately acute angles, straight to slightly curved, terminating at apex of lobes, sometimes only slightly thicker than secondary veins at first node. Secondary veins moderate-sized; 4–8 on central lobe and 1–3 on lateral lobes on leaves at first node, 6–15 on central lobe and 2–8 on lateral lobes at nodes 2–10, to 28 per lobe at later nodes; mostly alternate; mostly  $\frac{1}{6}$ – $\frac{1}{3}$  length of blade, rarely to  $\frac{2}{3}$  at first node, longest centrally on centre lobe; slightly curved; diverging at moderately acute angles; open, terminating at margin in tooth or sinus; impressed above, slightly raised below. Inter-secondary veins occasional. Tertiary veins reticulate. *Petioles* 10–200 mm long,  $\leq$  42 mm long at nodes 1–10; straight, circular in t.s.; shallowly channelled; glabrous below, densely minute- to short-pubescent above at early nodes becoming  $\pm$  glabrous except densely pubescent apically at later nodes; with abundant pearl bodies above and below. *Stipules* paired; 0.3–1.8 mm long at nodes 1–10, to 5 mm long at later nodes; simple; triangular, keeled; apex acute to acuminate; deciduous to  $\pm$  persistent, papery; short-pubescent along margin and at apex, with pearl bodies along margin; green becoming brown, with red-orange canals along margin.

**SAP.** Resinous, drying orange-brown in stems and roots.

**ODOUR.** Unpleasant in hypocotyl and roots.

**ARCHITECTURE.** Koriba's model (Hallé et al., 1978). Trunk axis initially monopodial and orthotropic to at least 81 cm tall; eventually sympodial, one of the 2–6 branches at each tier becoming erect (Hallé et al., 1978). Branches orthotropic,  $\pm$  verticillate (Hallé et al., 1978). No major branches were produced on our seedlings, all  $\leq$  81 cm tall. Proleptic branches, produced after apical meristem damaged, have 3–4 stipule-like scales toward base, produce several smaller leaves with fewer lobes than those formed before damage. Leaves held horizontal to descending.

### Ecology

**PHENOLOGY.** Fruits mature during the late dry season, mostly after March in Panama (Croat, 1978), about 1–2(–4) months after peak flowering, while the tree is leafless (Poppendieck, 1981; Janzen, 1983; Bullock & Solis-Magallanes, 1990). Most seeds are shed before the rainy season begins (Poppendieck, 1980).

**DISPERSAL.** When ripe, capsules are dry, with outer valves dark brown, spreading and alternating with yellow-brown

membranous inner valves. Seeds are wind-dispersed floaters (Augsburger, 1988), being gradually liberated from the partially opened fruit (Poppendieck, 1981). In Costa Rica, seeds are eaten by spiny pocket mice (Janzen et al., 1990).

**GERMINATION.** Seeds have hard, impermeable seed coats. The chalazal plug must become loosened before imbibition and germination can occur, which may occur rapidly by fires frequent in their secondary habitats or more slowly by other factors. Germination of freshly collected, untreated seeds was low in sun and shade ( $\leq$  17%), asynchronous over a 35 week period, and bimodal: a few seeds (4–9%) germinated in the first 3 weeks in sun (9 weeks in shade), the rest (8–12%) after a gap of 10–12 weeks. In a later seed collection, a hot water pretreatment increased germination over controls in both sun and shade (50% vs 4%): germination was still asynchronous (but not bimodal) over the 23 week period and was slightly faster in sun (7 weeks) than shade (9 weeks). Ricardi et al. (1987) also report low germination (7%) in the first three weeks. Seeds stored at room temperature were  $>$  95% viable after nearly 10 years (Garwood & Lighton, 1990), germinating in 7–10 days without treatments (Garwood, unpublished data).

**ESTABLISHMENT.** Seedlings are extremely shade intolerant and probably require large gaps to survive (Augsburger, 1984).

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## DISCUSSION

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The gross morphology of seeds of *Bixa urucurana* Willd. is very similar to that of *B. orellana* L. (Dathan & Singh, 1972; Corner, 1976), including a complex chalazal plug, an embryo with cotyledons asymmetrically bent under the chalazal plug, and a sarcotesta formed by large pigment-containing cells. Seeds of the five species in the genus differ slightly externally in size and colouring of the testal pigments (Baer, 1976). The dry seeds of *B. urucurana* are red-brown to orange-brown (Macbride, 1941; Molau, 1983; this study); when rehydrated, seeds from my collections became bright yellow. Dry seeds of *B. orellana* are usually orange-red or red (Macbride, 1941; Corner, 1976; Molau, 1983); when rehydrated, seeds from a commercial source (purchased at a Mexican-American grocery) turned bright red (Garwood, personal observation). These colour differences may reflect differences in the relative amounts of bixin, a reddish oil-soluble pigment, and orellin, a yellowish water-soluble pigment, in the testa. As there were few seeds on other BM collections of *B. urucurana*, I have not yet determined whether this trait is characteristic of the species.

Seeds of *Cochlospermum vitifolium* (Willd.) Spreng. are similar in gross morphology to those described for *C. religiosum* (L.) Alston (= *C. gossypium* DC., Poppendieck, 1980), including a complex chalazal plug, curved form with curved embryo, long testal hairs, and a thick tegmen (Dathan & Singh, 1972; Corner, 1976). Seeds of the other ten species in the genus are similar (Poppendieck, 1980). The unique and complex chalazal foramen and plug of the exotegmic seeds most strongly link the Cochlospermaceae and Bixaceae (Corner, 1976); other shared characters and differences between the two families are reviewed by Poppendieck (1980) and Cronquist (1981).

Seedlings of *Bixa urucurana* Willd. and *Cochlospermum vitifolium* (Willd.) Spreng. share the following characters: cotyledons are phanero-epigeal, foliaceous, persistent, petiolate, estipulate and glabrous; and leaves are simple, alternate and spiral, long-petiolate, stipulate, palmately veined, mostly ovate to widely ovate, and basally cordate at least at early nodes. Leaves of both species and cotyledons of *B. urucurana* contain idioblasts: these are discussed in more detail below. The two species differ in the following traits. The cotyledons of *B. urucurana* are ovate, palmately veined and conspicuously thick-lined (faintly pellucid) on the lower surface (see below), while those of *C. vitifolium* are narrowly ovate, pinnate-veined and lack lines or punctations, pellucid or not. All seedling and juvenile leaves of *B. urucurana* are entire and not lobed or parted, whereas the first leaves (eophylls) of *C. vitifolium* are irregularly serrate, usually 3-lobed or 3-cleft, and later juvenile leaves are 3- to 5-parted.

Previously published short descriptions of seedlings of *Cochlospermum vitifolium* agree with our description, except that Duke (1969) reported the cotyledon venation as uninnervated and Ricardi et al. (1987) did not detect stipules on the eophylls. These differences might be attributed to the fact that the primary and secondary veins are weak, but clearly visible under a strong light source, and the stipules fall off as the leaf expands, although a stipule scar is evident at the first node on my collections. A short description of the seedling of *Bixa orellana* L. (Duke, 1969) agrees with that given for *B. urucurana*, except that cotyledons are described as punctate-lineate and the illustrated cotyledons are widely ovate rather than ovate.

Leaves of *Bixa* and *Cochlospermum* have branched unicellular secretory idioblasts and canals in the spongy mesophyll (Keating, 1970). In leaves of *B. urucurana* seedlings, I found irregular, circular or elliptic pellucid punctations, < 0.1 mm long, which were sometimes associated with pellucid branched or unbranched canals. Punctations and canals were scarcely visible on the blade above (except when back-lit), but were conspicuous on the blade below, light orange-brown or green-brown. When back-lit, punctations were usually translucent yellow-green at early nodes to light orange-brown at later nodes, but sometimes opaque and dark brown-orange at later nodes. On the cotyledons, the idioblasts are much larger, to 0.5 × 0.1 mm long, thick and elongate, more or less parallel to the midvein; they were scarcely visible on the upper surface (even when back-lit), but conspicuously light yellow-brown below, and translucent brown-orange when back-lit. In leaves of *C. vitifolium* seedlings, I found faintly pellucid canals along the margins, which were absent or light yellow at early nodes to red-orange at later nodes. Similar canals were sometimes conspicuous throughout the blade of young expanding leaves at later nodes. No canals were found in the cotyledons.

Leaf pubescence differs greatly between the two genera (Keating, 1970; Poppendieck, 1980), with *Bixa* having multicellular peltate scales on the blade and veins of the leaf undersurface and *Cochlospermum* having unicellular simple hairs as well as multicellular globular hairs. On seedlings of *B. urucurana*, Dempsey & Garwood (1994) found that the peltate scales are much smaller and sparser than those on adults: they discuss the systematic significance of these ontogenetic changes.

The presence of multicellular globular hairs in *Cochlospermum vitifolium* has not been noted in standard floras (Robyns, 1967b; Croat, 1978; Poppendieck, 1981), although

they have been briefly discussed in anatomical studies and monographs of the family (Keating, 1970; Poppendieck, 1980). On seedlings of *C. vitifolium*, I found that the multicellular globular hairs were 0.050–0.075 mm in diameter and most abundant on the youngest stem internode, and on stipule margins, petioles and primary and secondary veins of expanding leaves, but often persisted on mature leaves and nodes. Globular hairs on young leaves of adult specimens examined at the BM were in the same size range (Garwood, personal observation; see also Keating, 1970: fig. 4), although Poppendieck (1980: fig. 46) illustrates hairs up to 0.5 mm in diameter; these were initially abundant, especially at the base of the primary vein, but fewer were found on mature leaves. Poppendieck (1980) and Keating (1970) called these hairs vestigial, but they might be fully functional 'pearl bodies' as described by O'Dowd (1982). Pearl bodies are typically 0.5–3.0 mm long, uni- or multi-cellular, spherical or club-shaped with short stems, easily detached from the leaf, lipid-rich, colourless to opaque, lustrous and 'pearl'-like, and often produced on the youngest leaves or near extrafloral nectaries or domatia; they occur primarily in tropical taxa, particularly those from second-growth habitats (O'Dowd, 1982). Because they are rapidly removed by ants in the field as a source of food, pearl bodies are often absent or scarce on plants in their natural habitats and on herbarium specimens. Except for their small size, the globular hairs on *C. vitifolium* fit the morphological description of pearl bodies. Documentation of removal by ants or mites (given their small size) and characterization of the cell contents will be necessary to confirm their biological function. Poppendieck (1980) assumed that they contained the same clear gum or resin as the fluid-containing idioblast canals of the leaf: this has not been reported for pearl bodies (O'Dowd, 1982).

Saplings of *Bixa urucurana* have large extra-floral nectaries below the stipule scar (Fig. 1R). I found glands were absent on the first ten leaf nodes above the cotyledons, but were well-developed and secretory above node 20. They actively secreted nectar when less than 3–4 nodes below the youngest leaf, then became inactive. Similar glands occur on adult specimens of *B. urucurana* and *B. orellana* examined at BM (Garwood, personal observation) and have been reported for all species of *Bixa* except *B. excelsa* Gleason & Krukoff (Baer, 1976). Ant attendance at similar glands on the fruit pedicel of *B. orellana* sensu lato increases the proportion of flowers maturing fruits (Bentley, 1977), because the species of ants present remove or deter flowering-eating insects. Ants attending the glands on the stems of saplings probably reduce leaf herbivory in a similar way. This is another vegetative trait of ecological importance not described in the standard floras (Macbride, 1941; Standley & Williams, 1961; Robyns, 1967a; Croat, 1978; Molau, 1983) or a recent field guide emphasizing vegetative characters (Gentry, 1993).

The seedling characters discussed above do not provide additional evidence for a closer link between the Bixaceae and Cochlospermaceae. Shared seedling-specific traits are usually those common throughout the angiosperms, such as petiolate, estipulate, foliaceous cotyledons. The taxa often differ in less wide-spread seedling-specific traits, such as the presence of pinnate venation or linear punctations in the cotyledons. Many of the vegetative differences and similarities noted by Keating (1970) and Poppendieck (1980) for adult stages, such as idioblasts, secretory canals, pubescence and leaf lobing, are already manifest at the early seedling stage.

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